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Intraspecific variation in aerobic and anaerobic locomotion: gilthead sea bream (*Sparus aurata*) and Trinidadian guppy (*Poecilia reticulata*) do not exhibit a trade-off between maximum sustained swimming speed and minimum cost of transport

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Intraspecific variation and trade-off in aerobic and anaerobic traits remain poorly understood in aquatic locomotion. Using gilthead sea bream (*Sparus aurata*) and Trinidadian guppy (*Poecilia reticulata*), both axial swimmers, this study tested four hypotheses: (1) gait transition from steady to unsteady (i.e., burst-assisted) swimming is associated with anaerobic metabolism evidenced as excess post exercise oxygen consumption (EPOC); (2) variation in swimming performance (critical swimming speed; U_{crit}) correlates with metabolic scope (MS) or anaerobic capacity (i.e., maximum EPOC); (3) there is a trade-off between maximum sustained swimming speed (U_{sus}) and minimum cost of transport (COT_{min}); and (4) variation in U_{sus} correlates positively with optimum swimming speed (U_{opt} ; i.e., the speed that minimizes energy expenditure per unit of distance traveled). Data collection involved swimming respirometry and video analysis. Results showed that anaerobic swimming costs (i.e., EPOC) increase linearly with the number of bursts in *S. aurata*, with each burst corresponding to $0.53 \text{ mg O}_2 \text{ kg}^{-1}$. Data are consistent with a previous study on striped surfperch (*Embiotoca lateralis*), a labriform swimmer, suggesting that the metabolic cost of burst swimming is similar across various types of locomotion. There was no correlation between U_{crit} and MS or anaerobic capacity in *S. aurata* indicating that other factors, including morphological or biomechanical traits, influenced U_{crit} . We found no evidence of a trade-off between U_{sus} and COT_{min} . In fact, data revealed significant negative correlations between U_{sus} and COT_{min} , suggesting that individuals with high U_{sus} also exhibit low COT_{min} . Finally, there were positive correlations between U_{sus} and U_{opt} . Our study demonstrates the energetic importance of anaerobic metabolism during unsteady swimming, and provides intraspecific evidence that superior maximum sustained swimming speed is associated with superior swimming economy and optimum speed.

Keywords: aerobic metabolic scope, anaerobic capacity, burst swimming, excess post exercise oxygen consumption, intraspecific variation and trade-off, locomotion, maximum sustained swimming speed, minimum cost of transport

Abbreviations: EPOC, Excess post exercise oxygen consumption; BL, Body length; COT, Cost of transport; COT_{min} , Minimum cost of transport; Exercise MO_2 , Metabolic rate measured in swimming fish (i.e., instantaneous metabolic rate); MO_2 , Metabolic rate; $MO_{2active}$, Active metabolic rate defined as the maximum metabolic rate maintained for 0.5 h; MO_{2max} , Maximum metabolic rate defined as the maximum metabolic rate measured at increasing swimming speeds; $MO_{2routine}$, Routine metabolic rate defined as the average metabolic rate in fish swimming at 0.5 BL s^{-1} ; MO_{2stand} , Standard metabolic rate (i.e., a in Equation 2); MO_{2sus} , Maximum sustained metabolic rate defined as the maximum metabolic rate (over 0.5 h) without any EPOC (i.e., no influence of anaerobic metabolism); Total MO_2 , Exercise MO_2 and EPOC combined as an estimate of the total metabolic swimming cost; U_{active} , Swimming speed associated with the active metabolic rate

INTRODUCTION

Variation in locomotor performance and metabolism is linked to fitness, because both traits are often coupled with important behaviors such as predator evasion, prey capture, reproduction,

($MO_{2active}$); U_{crit} , Critical swimming speed; U_{max} , Swimming speed associated with the maximum metabolic rate (MO_{2max}); U_{opt} , Optimum swimming speed defined as the speed that minimizes energy expenditure per unit of distance traveled; U_{sus} , Maximum sustained swimming speed defined as the maximum recorded swimming speed (over 0.5 h) without any EPOC (i.e., no influence of anaerobic metabolism).

migration, and dominance (Clobert et al., 2000; Walker et al., 2005; Langerhans, 2009a; Leis et al., 2009; Eliason et al., 2011; Seebacher et al., 2013; Wilson et al., 2013; Burnett et al., 2014; Killen et al., 2014; Scantlebury et al., 2014). Intraspecific variation in locomotor performance and metabolism is repeatable across time and environments (Chappell and Odell, 2004; Claireaux et al., 2005, 2007; Oufiero and Garland, 2009; Norin and Malte, 2011, 2012; Careau et al., 2014) and may be heritable and/or trans-generational (Rønning et al., 2007; Dalziel et al., 2011, 2012; Dalziel and Schulte, 2012; Gore and Burggren, 2012; McKenzie et al., 2013; Mattila and Hanski, 2014), indicating that traits related to locomotor performance and metabolism are subjected to natural selection and could evolve over time.

Performance trade-offs are central to understanding the vast phenotypic variation found among species, populations, and individuals. Trade-offs may occur when two antagonistic traits cannot be optimized simultaneously, because the two traits pose conflicting demands on the same design feature (Damme et al., 2002). Consequently, excellence in one trait will come at the cost of performance in the other trait (Vanhooydonck et al., 2014). Hence, an organism may specialize in one trait at the cost of the other, in which case a trade-off may cause phenotypic differentiation (DeWitt and Scheiner, 2004; Konuma and Chiba, 2007; Herrel et al., 2009). Alternatively, the conflicting demands may result in organisms performing sub-optimally for both traits and therefore, constrain evolution (Lewontin, 1978; Arnold, 1992). In fish, there is evidence of a trade-off between endurance capacity and sprint speed (Langerhans, 2009b; Oufiero et al., 2011); however, the trade-off is not ubiquitous at the whole-organism level (Wilson et al., 2002; Vanhooydonck et al., 2014; Fu et al., 2015).

Levels of swimming exercise in fishes have been divided into three categories on the basis of the time a given speed can be maintained before the onset of fatigue (Beamish, 1978): sustained (more than 200 min), prolonged (20 s to 200 min) and burst swimming (less than 20 s). In many teleosts, the segmented myotomal musculature is distinctively divided into red oxidative (slow-twitch) muscles and white glycolytic (fast-twitch) muscles. Red muscles are powered by oxidative phosphorylation, whereas white muscles are largely powered by anaerobic utilization of phosphocreatine, ATP and glycogen. At sustainable swimming speeds, the red musculature is powering propulsion, whereas white musculature is increasingly recruited for propulsion at faster speeds. Employing white musculature for burst-assisted swimming typically involves significant physiological perturbations including decreasing levels of intracellular pH (Lurman et al., 2007) and muscle glycogen (Peake and Farrell, 2004), and increasing levels of lactate (Martínez et al., 2004; Peake and Farrell, 2004) and inorganic phosphate (Lurman et al., 2007) indicating a non-steady state and partial reliance on anaerobic metabolism. While metabolic locomotor cost during sustained swimming has received considerable attention (Brett, 1964; Steinhausen et al., 2005; Ohlberger et al., 2006; Svendsen et al., 2013), the metabolic cost during non-steady burst swimming remains poorly understood. Metabolic locomotor cost during sustained swimming can be estimated using measurements of instantaneous oxygen consumption rates (exercise MO_2), whereas metabolic cost during unsustainable swimming can be

estimated by combining exercise MO_2 with excess post exercise oxygen consumption (EPOC). The presence of EPOC is considered evidence of anaerobic activity in intact fish (Beamish, 1978), with many of the physiological perturbations related to anaerobic metabolism cleared during the period associated with EPOC (Peake and Farrell, 2004). In striped surf perch (*Embiotoca lateralis*), a labriform swimmer, there is a linear relationship between the number of bursts and EPOC, with EPOC constituting 25% of the total swimming costs (total MO_2 ; i.e., exercise MO_2 and EPOC combined) on average (Svendsen et al., 2010). In contrast, the metabolic cost of burst swimming in axial swimmers is largely unknown (Puckett and Dill, 1984; Farrell, 2007).

Standard metabolic rate ($MO_{2\text{stand}}$) is a basic maintenance requirement measured as the minimum rate of oxygen consumption of postprandial unstressed animals at rest, below which physiological function is impaired. Long-term energy demands for swimming, food acquisition and treatment, regulation owing to environmental perturbations, and reproduction are additional to standard metabolism. These demands are met within the range set by the maximum metabolic rate ($MO_{2\text{max}}$) (Priede, 1985). The difference between $MO_{2\text{stand}}$ and $MO_{2\text{max}}$ is termed the metabolic scope (MS). Because MS is strongly influenced by environmental variables, including temperature and oxygen availability, MS is predicted to be a major physiological variable in relation to climate change and aquatic hypoxia (Claireaux and Lefrançois, 2007; Chabot and Claireaux, 2008; Guderley and Pörtner, 2010; Pörtner, 2010; Pörtner and Peck, 2010; Di Santo, 2015). Nevertheless, intraspecific relationships between MS and other important physiological traits have rarely been explored in detail. MS and swimming performance correlate positively in intraspecific comparisons involving disparate populations of Atlantic silverside (*Menidia menidia*) (Arnott et al., 2006) and rainbow trout (*Oncorhynchus mykiss*) (Claireaux et al., 2005), but it remains uncertain to what extent the relationship is found in other species.

Locomotor performance and associated metabolic costs are often coupled with life history traits, which may involve trade-offs related to growth and $MO_{2\text{stand}}$ (Arnott et al., 2006; Rouleau et al., 2010). Recently, it was suggested that a trade-off between maximum sustained swimming speed (U_{sus}) and minimum cost of transport (COT_{min}) may be driving morphological diversity in axial swimmers including teleosts and cetaceans (Tokić and Yue, 2012). The trade-off assumes constraints in optimizing both U_{sus} and COT_{min} and suggests that aquatic species optimize either U_{sus} or COT_{min} . Tokić and Yue (2012) applied the trade-off to models of morphological variation and reported congruent morphological variation in a number of extant aquatic species. While the trade-off may explain interspecific morphological variation, the trade-off has not been examined empirically at the intraspecific level. Likewise, it is not known if intraspecific diversity in U_{sus} is a source of variation in optimum swimming speed (U_{opt}), i.e., the speed that minimizes energy expenditure per unit of distance traveled.

Using gilthead sea bream (*Sparus aurata*), *E. lateralis* and Trinidadian guppy (*Poecilia reticulata*), we employed swimming respirometry and video analyses to test four hypotheses: (1) burst activity is an indicator of anaerobic power production and

correlates positively with the presence and magnitude of EPOC; (2) intraspecific diversity in MS or anaerobic capacity correlates positively with swimming performance; (3) there is a trade-off between U_{sus} and COT_{min} such that a high value of U_{sus} is associated with a high value of COT_{min} at the intraspecific level, and (4) variation in U_{sus} correlates positively with U_{opt} . Data on *S. aurata* were collected for the present study, whereas data on *E. lateralis* and *P. reticulata* were derived from previous studies (Svendsen et al., 2010, 2013).

MATERIALS AND METHODS

ANIMALS

A total of 13 gilthead sea bream (*Sparus aurata*) (body mass: 79.77 ± 2.38 g; standard length: 14.79 ± 0.24 cm (mean \pm SE)) were obtained from a fish farm (Ferme Marine de Douhet) in France and kept in a flow-through holding tank (0.7 m^3) with saltwater (30‰) at $10 \pm 1^\circ\text{C}$ at the University of Copenhagen in Denmark. *S. aurata* were fed daily with commercial trout pellets (Biomar, Brande, Denmark). All methods applied in the present study were in agreement with current Danish regulations for the treatment and welfare of experimental animals. No fish were used more than once, and there was no mortality during any of the tests.

RESPIROMETRY

A swimming respirometer (8.24 L) was used to measure oxygen consumption rate (MO_2 ; $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) as a function of swimming speed (U). Water temperature inside the respirometer was maintained at 10.0°C (range: 9.9 – 10.1°C) using a temperature controlling instrument (TMP-REG; Loligo Systems; Tjele, Denmark). The respirometer was submerged in an ambient tank supplying water for the respirometer. Air stones maintained oxygen levels $>95\%$ air saturation in the ambient tank, and the water was recirculated through a loop consisting of a separate biological filter and a UV sterilizer (model UV-1000; Tetra Pond, Melle, Germany).

The swimming section of the respirometer was $32 \times 9 \times 11$ cm (L \times W \times H). An impeller placed downstream of the swimming section was driven by an external electric motor that generated a re-circulating flow. Deflectors situated upstream of the swimming section collimated the flow. To promote rectilinear flow and a uniform velocity profile in the swimming section, water passed through an upstream honeycomb (7 mm cell diameter; Plascor Inc., Michigan, USA) producing a micro turbulent flow. A grid (10 mm) in the downstream direction bounded the swimming section. A vane wheel flow sensor (Höntzsch GmbH, Waiblingen, Germany) was used to measure water speeds in the swimming section. The measurements were used for a linear correlation between water speed and voltage output from the external motor controller.

Oxygen partial pressure (kPa) in the respirometer was measured using fiber optic sensor technology (PreSens, Regensburg, Germany). Intermittent flow respirometry was applied in accordance with previous studies (Steffensen, 1989). A computer-actuated pump was employed to replace water in the respirometer through a chimney as described previously (Svendsen et al., 2013). The software AutoResp (Loligo Systems Aps, Tjele, Denmark) was used to control the flush (240 s), wait

(120 s) and measurement (540 s) phases. The settings provided one measurement of MO_2 per 15 min. The declining oxygen partial pressure (kPa) during the measurement phase was used to calculate MO_2 ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) using the equation:

$$\text{MO}_2 = \frac{K V \beta}{M} \quad (1)$$

where K is the linear rate of decline (kPa h^{-1}) in the oxygen content over time (h) in the respirometer, V is the volume of the respirometer (L) corrected for the volume of fish, β is the solubility of oxygen in the water ($\text{mg O}_2 \text{ L}^{-1} \text{ kPa}^{-1}$) ($\beta = 0.4480$) and M is the body mass of the fish (kg).

Preliminary trials demonstrated that the variation explained (R^2) by the linear equation fitted to the declining oxygen content (kPa h^{-1}), associated with each MO_2 measurement, was always ≥ 0.95 , similar to previous studies (Claireaux et al., 2006; Svendsen et al., 2012). The oxygen content never fell below 17.6 kPa. Levels of background respiration (i.e., microbial respiration) were estimated from blank runs and used to correct MO_2 measurements (Jones et al., 2007; Svendsen et al., 2014).

BURST SWIMMING

Individual fish in the swimming section were recorded dorsally using a Hitachi video camera (model VM-H630E; Düsseldorf, Germany), situated above the swimming respirometer. A Pinnacle frame grabber (model PCTV USB2; Corel Corporation, Ontario, Canada) continuously transferred recordings to a PC, and fish 2D position (x, y coordinates) was tracked at 25 Hz using the software LoliTrack (Loligo Systems, Tjele, Denmark). A burst was defined as a forward excursion (≥ 4 cm) with the swimming speed increasing $\geq 5 \text{ cm s}^{-1}$. The number of bursts was determined over 3 min per respirometric loop (each 15 min) and used to estimate the total number of bursts per swimming speed (each 30 min; see below).

EXPERIMENTAL PROTOCOL

S. aurata for experiments were fasted for 48 h prior to respirometry to ensure a post-absorptive state. Fish mass (to nearest 0.01 g), length, depth and width (all to nearest 1 mm) were measured for pre-experimental calculation and correction of the solid blocking effects (Bell and Terhune, 1970; Gehrkel et al., 1990). Fish were acclimated to the respirometer for 12 h (overnight) while swimming at 0.5 body lengths per second (BL s^{-1}) prior to collection of data.

After the acclimation period, routine MO_2 ($\text{MO}_{2\text{routine}}$) was estimated as the average MO_2 during eight consecutive respirometric loops (i.e., 2 h) for each individual *S. aurata* swimming at 0.5 BL s^{-1} (i.e., acclimation speed) (Svendsen et al., 2010). At the individual level, the standard deviation (SD) of $\text{MO}_{2\text{routine}}$ was calculated using the eight MO_2 measurements. Next, *S. aurata* were exposed to progressive increments in the swimming speed of 0.5 BL s^{-1} every 30 min up to 2 BL s^{-1} . Using 30 min intervals for each swimming speed is a common approach (Schurmann and Steffensen, 1997; McKenzie et al., 2003, 2004; Lurman et al., 2007). Two measures of MO_2 were collected at each swimming speed. After completing measurements at 2 BL s^{-1} , *S. aurata* were exposed to speed increments of 0.25 BL s^{-1} every 30 min.

To examine the presence and magnitude of EPOC, the swimming speed was reduced to 0.5 BL s^{-1} (acclimation speed) after each exercise level from 2 BL s^{-1} and onwards. Specifically, detection of EPOC was carried out by comparing individual $MO_{2\text{routine}} + \text{SD}$ with the first post exercise MO_2 measurement during the 0.5 BL s^{-1} period that followed each new swimming exercise (Svendsen et al., 2010). It was considered evidence of EPOC if the first post exercise MO_2 was above $MO_{2\text{routine}} + \text{SD}$. The measurements of MO_2 at 0.5 BL s^{-1} were continued until the MO_2 was below $MO_{2\text{routine}} + \text{SD}$. When the MO_2 stabilized below $MO_{2\text{routine}} + \text{SD}$, the swimming speed was increased to the next exercise level (i.e., the previous exercise speed + 0.25 BL s^{-1}). The protocol involving incrementally increasing swimming speeds followed by the procedure to detect EPOC was continued until fatigue.

DATA ACQUISITION AND ANALYSIS

Exercise MO_2 was recorded at increasing speeds from 0.5 BL s^{-1} to fatigue. Exercise MO_2 as a function of U in individual fish was described by the exponential equation:

$$MO_2 = a \exp(Ub) \quad (2)$$

where a is the MO_2 at zero speed ($U = 0$) and b is the rate of increase in the MO_2 as a function of U . The intercept with the y-axis (a) provides an estimate of the standard metabolic rate ($MO_{2\text{stand}}$) (Brett, 1964; Arnott et al., 2006; Svendsen et al., 2013). The analyses included a comparable data set on *P. reticulata* from an earlier study (Svendsen et al., 2013) in addition to the collected data on *S. aurata*. Following Svendsen et al. (2013), model fittings were limited to swim speeds without burst-assisted swimming. The analysis disregarded the measurements of post exercise MO_2 at 0.5 BL s^{-1} that were inserted to evaluate EPOC after swimming speeds $\geq 2 \text{ BL s}^{-1}$. Equation (2) was fitted to the individual data sets using mixed-effect models to account for temporal autocorrelation due to the repeated measurements. The analysis included an AR1 (autoregressive of order 1) covariance structure.

Maximum sustained (or aerobic) metabolic rate ($MO_{2\text{sus}}$) is defined as the maximum metabolic rate that can be maintained aerobically without the accumulation of anaerobic metabolic products that contribute to fatigue and negatively impact endurance (Hillman et al., 2014). In the present study, EPOC was detected when post exercise MO_2 was above $MO_{2\text{routine}} + \text{SD}$, indicating anaerobic metabolism. At the individual level, $MO_{2\text{sus}}$ was measured as the maximum recorded metabolic rate (over 0.5 h) at increasing swimming speeds without evidence of EPOC. The concurrent swimming speed was used as an estimate of the maximum sustained swimming speed (U_{sus}).

Active metabolic rate ($MO_{2\text{active}}$) was defined as the maximum exercise MO_2 that *S. aurata* maintained for 0.5 h without fatigue (Schurmann and Steffensen, 1997; Claireaux et al., 2005). Maximum metabolic rate ($MO_{2\text{max}}$) was defined as the highest exercise MO_2 measured during the complete swimming protocol (McKenzie et al., 2003; Svendsen et al., 2013; Binning et al., 2014). $MO_{2\text{active}}$ and $MO_{2\text{max}}$ may be different, because $MO_{2\text{active}}$ is measured over 30 min , whereas $MO_{2\text{max}}$ is often measured over

a shorter period of time (minimum 15 min ; one respirometric loop) and at a higher swim speed.

$MO_{2\text{active}}$ is usually assumed to be the maximum aerobic metabolic rate (Schurmann and Steffensen, 1997); however, to what extent $MO_{2\text{active}}$ includes an anaerobic component remains uncertain. If $MO_{2\text{active}}$ is the maximum aerobic metabolic rate, $MO_{2\text{active}}$ should not differ significantly from $MO_{2\text{sus}}$. To clarify differences between metabolic rates, a one way repeated measure ANOVA was used to compare $MO_{2\text{stand}}$, $MO_{2\text{sus}}$, $MO_{2\text{active}}$, and $MO_{2\text{max}}$. The test was followed by all pairwise comparison procedures (Holm-Šidák). The same test was employed to compare the swimming speeds associated with $MO_{2\text{sus}}$, $MO_{2\text{active}}$, and $MO_{2\text{max}}$ (i.e., U_{sus} , U_{active} , and U_{max}).

The method described by Brett (1964) was used to calculate the critical swimming speed (U_{crit}). The protocol provides measurements that are repeatable in individual fish, suggesting that U_{crit} represent a measure of performance, which is a lasting characteristic of the organism (Claireaux et al., 2007; Oufiero and Garland, 2009).

The magnitude of EPOC ($\text{mg O}_2 \text{ kg}^{-1}$) was quantified using protocols published previously (Svendsen et al., 2010). When EPOC was detected, the individual relationship between time t (h) and post exercise MO_2 was described using a double exponential equation:

$$MO_2 = a \exp(bt) + c \exp(dt) + MO_{2\text{routine}} \quad (3)$$

where a , b , c , and d are constants estimated using non-linear regression. Data included the exercise MO_2 at $t = 0$. The recovery period was terminated when the fitted curve intercepted $MO_{2\text{routine}} + \text{SD}$ and provided an estimate of recovery time (h). EPOC magnitude was calculated as the integrated area between the fitted curve (Equation 3) and $MO_{2\text{routine}}$ from $t = 0$ to the end of the recovery period. At the individual level, EPOC was combined with the exercise MO_2 to provide an estimate of the total cost of swimming (total MO_2 ; $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), covering both aerobic and anaerobic components. The anaerobic capacity was estimated as the maximum EPOC observed in individual fish. Anaerobic capacity was quantified as $\text{mg O}_2 \text{ kg}^{-1}$ and $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$.

To test if the onset of burst swimming is a reliable predictor of the onset of EPOC, the minimum speed with burst swimming was correlated with the minimum speed with EPOC. The analysis was carried out using linear least square regression.

Linear mixed effects models were used to examine the relationship between the number of bursts and the magnitude of EPOC ($\text{mg O}_2 \text{ kg}^{-1}$). Models included swimming speed as a covariate and interaction terms for swimming speed, burst number and fish identity. Temporal autocorrelation due to repeated measures was accounted for by including an AR1 covariance structure. The analysis included a comparable data set on *E. lateralis* from an earlier study (Svendsen et al., 2010).

The metabolic scope was calculated as $MO_{2\text{max}} - MO_{2\text{stand}}$ in individual fish. The hypothesis that swimming performance (U_{crit}) is correlated with metabolic scope or anaerobic capacity in individual fish was tested using linear least square regression.

Cost of transport (COT) was calculated as $\text{mg O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ using the equation:

$$\text{COT} = \frac{\text{MO}_2}{U} \quad (4)$$

where MO_2 is the metabolic rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), and U is the corresponding swimming speed (m h^{-1}). The relationship between swimming speed and COT is usually U or \cup shaped with high COT values at low and high swimming speeds (Rouleau et al., 2010).

For each individual fish, COT_{\min} was measured using two different approaches: (A) COT_{\min} was estimated as the lowest recorded value of COT. Following this approach, the optimum swimming speed (U_{opt} ; the speed that minimizes energy expenditure per unit of distance traveled) was estimated as the swimming speed that corresponded to COT_{\min} ; (B) COT_{\min} was estimated by first determining U_{opt} using the equation:

$$U_{\text{opt}} = \frac{1}{b} \quad (5)$$

where b originates from Equation (2) describing the individual relationship between swimming speed (cm s^{-1}) and MO_2 ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$). Next, MO_2 at U_{opt} was calculated using Equation (2); and then COT_{\min} was derived using Equation (4). Results from both approaches (A and B) to estimate COT_{\min} and U_{opt} are reported, but figures are based on approach A. The analyses included a comparable data set on *P. reticulata* from an earlier study (Svendsen et al., 2013).

In a modeling study, Tokić and Yue (2012) presented evidence for a trade-off between U_{sus} and COT_{\min} . The trade-off predicts a positive correlation between U_{sus} and COT_{\min} , i.e., superior sustained swimming performance is associated with inferior swimming economy. To examine the trade-off in *S. aurata*, individual measures of U_{sus} and COT_{\min} were correlated using linear least square regression. Similarly, this study tested for a relationship between U_{sus} and U_{opt} in individual fish. In addition to the data on *S. aurata*, the analyses of U_{sus} , COT_{\min} , and U_{opt} included a comparable data set derived from an earlier study on *P. reticulata* (Svendsen et al., 2013).

Data were transformed [e.g., $\ln(x + 1)$] to meet the normality and homoscedasticity requirements of parametric analyses. The free statistical software R (R Development Core Team, 2014) and SigmaPlot (Systat Software, Erkrath, Germany) were used for statistical analyses and graphing. The R package nlme (Pinheiro et al., 2011) was employed to fit models. Results were considered significant at $P < 0.05$. All values are reported as means \pm SE unless otherwise noted.

RESULTS

METABOLIC RATES AND SWIMMING PERFORMANCE

$\text{MO}_{2\text{stand}}$, $\text{MO}_{2\text{sus}}$, $\text{MO}_{2\text{active}}$, and $\text{MO}_{2\text{max}}$ were measured at increasing speeds (Figure 1) and were all statistically different ($P < 0.05$). Notably, $\text{MO}_{2\text{sus}}$ was lower than $\text{MO}_{2\text{active}}$, providing evidence of anaerobic metabolism (EPOC) in a significant number of *S. aurata* exercising at the level of $\text{MO}_{2\text{active}}$ (Figure 1A). The finding suggests that $\text{MO}_{2\text{sus}}$ is a more appropriate measure of maximum sustained (or aerobic) metabolic

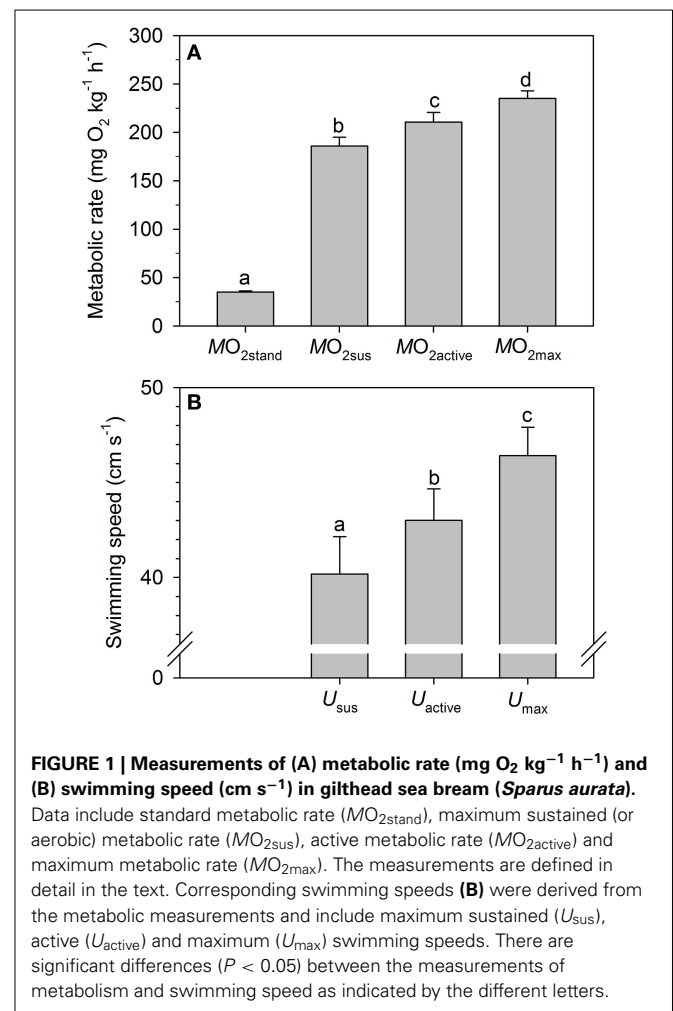


FIGURE 1 | Measurements of (A) metabolic rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) and (B) swimming speed (cm s^{-1}) in gilthead sea bream (*Sparus aurata*). Data include standard metabolic rate ($\text{MO}_{2\text{stand}}$), maximum sustained (or aerobic) metabolic rate ($\text{MO}_{2\text{sus}}$), active metabolic rate ($\text{MO}_{2\text{active}}$) and maximum metabolic rate ($\text{MO}_{2\text{max}}$). The measurements are defined in detail in the text. Corresponding swimming speeds (B) were derived from the metabolic measurements and include maximum sustained (U_{sus}), active (U_{active}) and maximum (U_{max}) swimming speeds. There are significant differences ($P < 0.05$) between the measurements of metabolism and swimming speed as indicated by the different letters.

rate than $\text{MO}_{2\text{active}}$. Similar to the metabolic values, the corresponding swimming speeds (U_{sus} , U_{active} , and U_{max}) differed significantly ($P < 0.05$) (Figure 1B). Interestingly, U_{sus} varied twofold between individuals with measurements ranging between 27 and 53.2 cm s^{-1} . Measures of U_{crit} were not included in Figure 1, but ranged between 35.3 and 56.5 cm s^{-1} , with an average value of $45.0 \pm 1.6 \text{ cm s}^{-1}$. $\text{MO}_{2\text{sus}}$ and U_{sus} corresponded to $79.3 \pm 3.3\%$ of $\text{MO}_{2\text{max}}$ and $88.9 \pm 1.9\%$ of U_{crit} , respectively, with anaerobic metabolism detected above these exercise levels.

EXERCISE MO_2 AND TOTAL MO_2 IN RELATION TO U_{crit}

EPOC was detected at all swimming speeds faster than U_{sus} and was combined with the exercise MO_2 to estimate the total MO_2 . Because of the observed intraspecific variation in swimming performance, exercise MO_2 and total MO_2 were plotted as a function of $\%U_{\text{crit}}$ (Figure 2A) similar to previous studies (Lurman et al., 2007; Tudorache et al., 2008; Teulier et al., 2013). EPOC contributed to the total MO_2 starting at 86% of U_{crit} (Figure 2A). EPOC constituted $53.5 \pm 4.9\%$ of the total MO_2 , ranging from 14.2 to 86.4% of total MO_2 , at swimming speeds with evident EPOC. Thus, EPOC frequently constituted more than half of the swimming costs. Recovery time associated with EPOC lasted $7.8 \pm 1.1 \text{ h}$, ranging from 1.0 to 20.9 h (Figure 2B).

POSITIVE CORRELATIONS BETWEEN BURST ACTIVITY AND ANAEROBIC METABOLISM (EPOC)

There was a positive linear relationship ($P < 0.0001$; $R^2 > 0.95$) between the minimum speed with EPOC and the minimum speed with burst swimming (Figure 3). The intercept with the y-axis was not significantly different from zero ($P > 0.65$). The relationship shows that the onset of burst swimming is a strong predictor of the onset of EPOC and anaerobic metabolism at increasing swimming speeds.

The relationship between the number of bursts and magnitude of EPOC was examined using a linear mixed effects model. The model included swimming speed as a covariate, but no significant effect ($P > 0.25$) or interactions ($P > 0.64$) related to swimming speed was detected. Model terms for swimming speed and interactions were therefore eliminated from further analyses. A comparable data set from a previous study on *E. lateralis* (Svendsen et al., 2010) was included in the analysis. For both data sets, the intercept with y-axis was not significantly different from zero ($P > 0.34$) and the slopes did not differ between the two data sets ($P > 0.94$). These findings indicated that the relationships between burst numbers and EPOC were similar in the two species, and the data were therefore, combined. The resulting common relationship (Figure 4) was described by the equation ($P < 0.0001$):

$$EPOC = 0.53 (\pm 0.05) \text{ bursts} \quad (6)$$

The relationship indicates that each burst corresponds to an average metabolic cost of $0.53 \text{ mg O}_2 \text{ kg}^{-1}$ (Figure 4).

NO CORRELATION BETWEEN U_{crit} AND METABOLIC SCOPE OR ANAEROBIC CAPACITY

Metabolic scope was estimated as $MO_{2\text{max}} - MO_{2\text{stand}}$, whereas anaerobic capacity was estimated as the maximum EPOC observed in individual fish. The maximum EPOC value was always associated with fish fatigue. There was no evidence that individual U_{crit} correlated with metabolic scope ($P > 0.87$; $R^2 <$

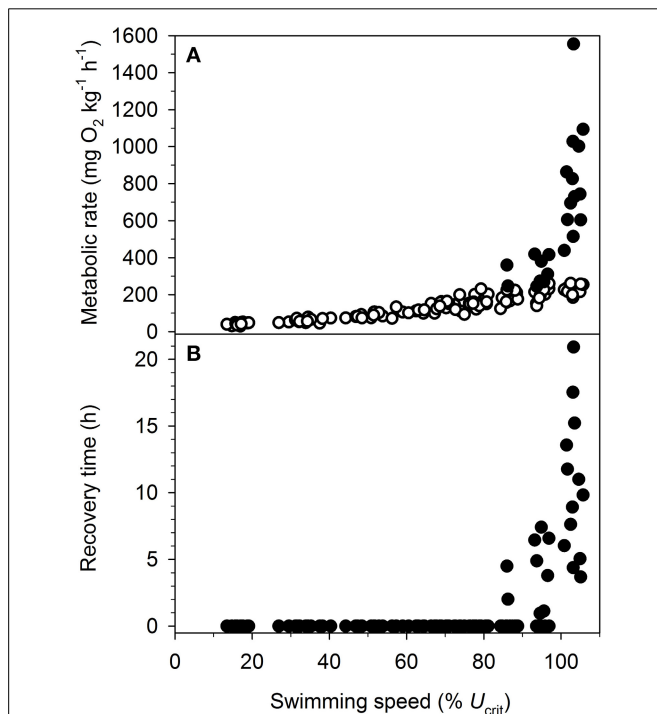


FIGURE 2 | (A) Metabolic rate ($\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) and **(B)** recovery time (h) in relation to swimming speed (% U_{crit}) in individual gilthead sea bream (*Sparus aurata*). U_{crit} is the critical swimming speed and defined in detail in the text. For **(A)**, metabolic rates were measured in the swimming fish (exercise MO_2 ; open symbols) and as excess post exercise oxygen consumption (EPOC; $\text{mg O}_2 \text{ kg}^{-1}$). Exercise MO_2 and EPOC were combined to estimate the total metabolic cost of swimming (total MO_2 ; closed symbols). For **(B)**, recovery time (h) reflects the duration of EPOC after single swimming exercises (up to 30 min).

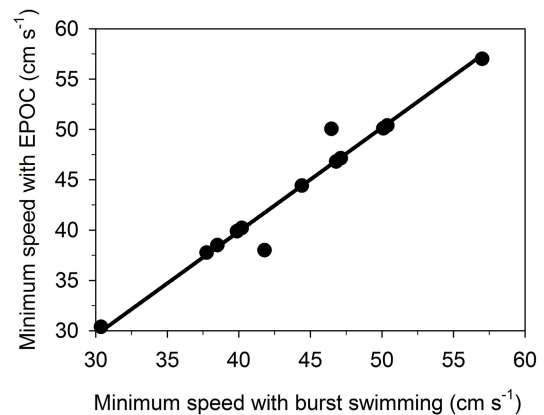


FIGURE 3 | The minimum speed with excess post exercise oxygen consumption (EPOC; $\text{mg O}_2 \text{ kg}^{-1}$) correlates positively with the minimum speed with burst swimming ($P < 0.0001$; $R^2 > 0.95$) in gilthead sea bream (*Sparus aurata*). The relationship shows that the onset of burst swimming at increasing speeds indicates the onset of EPOC and therefore, anaerobic metabolism in individual fish.

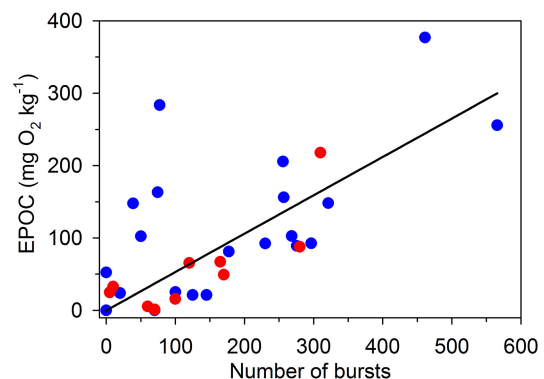


FIGURE 4 | The magnitude of excess post exercise oxygen consumption (EPOC; $\text{mg O}_2 \text{ kg}^{-1}$) correlates positively with burst activity in gilthead sea bream (*Sparus aurata*) (blue symbols) and striped surperch (*Embiotoca lateralis*) (red symbols). Data on *S. aurata* are from the present study, whereas data on *E. lateralis* are from Svendsen et al. (2010). The linear fit ($P < 0.0001$) reflects the pooled data set for both species (Equation 6), because species-specific regression slopes and intercepts with the y-axes are not statistically different ($P > 0.34$). The relationship suggests that a burst represents a metabolic cost of $0.53 \text{ mg O}_2 \text{ kg}^{-1}$.

0.01) or with anaerobic capacity ($P > 0.57$; $R^2 < 0.04$) (data not shown). The analyses of anaerobic capacity involved maximum EPOC quantified as $\text{mg O}_2 \text{ kg}^{-1}$ and $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$.

NO TRADE-OFF BETWEEN U_{sus} AND COT_{min}

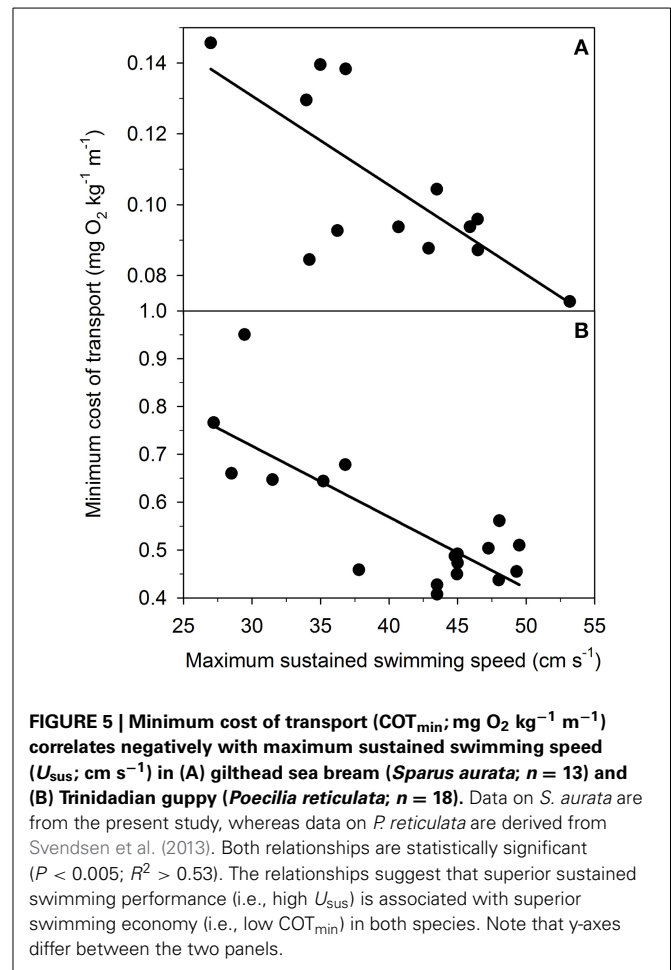
This study examined a trade-off between U_{sus} and COT_{min} by comparing swimming performance and metabolism in *S. aurata* and *P. reticulata*. In terms of *S. aurata*, U_{sus} was assumed to correspond to the highest swimming speed without EPOC (Figures 1, 2). Data on *P. reticulata* were derived from Svendsen et al. (2013). While EPOC was not measured in *P. reticulata*, the study quantified burst activity in individual *P. reticulata* at increasing speeds. Using the relationship between the onset of burst swimming and the onset of EPOC (Figure 3), EPOC occurrence at increasing speeds, and thereby U_{sus} , were estimated in individual *P. reticulata*. COT_{min} in *P. reticulata* was estimated in the same fashions (approaches A and B) as in *S. aurata* (Equations 4 and 5). The relationships between U_{sus} and COT_{min} were examined using linear least square regressions (Figure 5). For both species, there was no evidence of a trade-off between U_{sus} and COT_{min} . In fact, there were significant negative correlations between U_{sus} and COT_{min} , revealing that individuals exhibiting superior sustained swimming performance (i.e., high U_{sus}) also exhibit superior swimming economy (i.e., low COT_{min}) (Figure 5). The negative correlations between U_{sus} and COT_{min} were evident in both species and regardless of the approach (A and B) used to estimate COT_{min} (all $P < 0.005$; $R^2 > 0.53$). Data in Figure 5 are based on approach A.

POSITIVE CORRELATIONS BETWEEN U_{sus} AND U_{opt}

There were significant positive correlations between U_{sus} and U_{opt} (Figure 6). The analyses included data on *S. aurata* (Figure 6A) and *P. reticulata* (Figure 6B) and revealed that individuals exhibiting superior sustained swimming performance (i.e., high U_{sus}) also exhibit superior optimum swim speed (i.e., high U_{opt}). The positive correlations between U_{sus} and U_{opt} were evident in both species and regardless of the approach used to estimate U_{opt} (approach A: all $P < 0.005$; $R^2 > 0.40$; approach B: all $P < 0.05$; $R^2 > 0.26$). Data in Figure 6 are based on approach A.

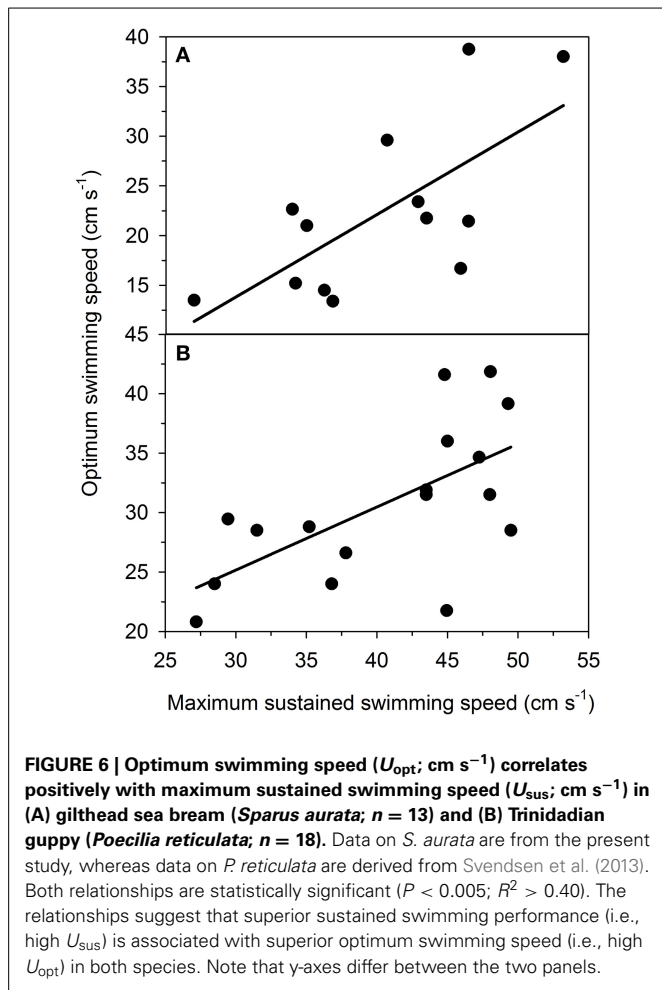
DISCUSSION

This study demonstrated the energetic importance of anaerobic metabolism during unsteady locomotion. There was no evidence of U_{crit} correlating with MS or anaerobic capacity. Moreover, we provided intraspecific evidence that a high U_{sus} is coupled with low COT_{min} and high U_{opt} in individual fish. Specifically, our results reveal that burst swimming is associated with anaerobic metabolism and a substantial metabolic cost, which is expressed as EPOC. Our intraspecific results on two teleost species are at odds with the conjecture that there is a trade-off between U_{sus} and COT_{min} as indicated by Tokić and Yue (2012). By applying the trade-off, the authors provided a model that explained variation in morphology in various teleost and cetacean species. In contrast, the present study is based on intraspecific data collected empirically. Our findings suggest that intraspecific variation in U_{sus} and COT_{min} is not driven by a trade-off producing a high U_{sus} in some individuals and a low COT_{min} in other individuals.



Because the results suggest that U_{sus} and COT_{min} are optimized concurrently, it is unlikely that the trade-off drives intraspecific morphological variation.

Previous studies have demonstrated that the U_{crit} protocol includes swimming powered by both aerobic and anaerobic metabolism (Burgetz et al., 1998; Richards et al., 2002). In *E. latralis*, EPOC and anaerobic metabolism is present at 88% of U_{crit} (Svendsen et al., 2010). Corroborating previous results, the present study found evidence of EPOC starting at swimming speeds corresponding to 86% of U_{crit} . At higher speeds, EPOC increased rapidly and constituted up to 86% of the total MO_2 . The maximum value of EPOC was always associated with fatigue. Likewise, beginning at 89% of U_{crit} in Atlantic cod (*Gadus morhua*), Lurman et al. (2007) found evidence of anaerobic metabolism as indicated by decreasing levels of phosphocreatine and intracellular pH and increasing levels of inorganic phosphate. Our study corroborates that the U_{crit} protocol involves depletion of both aerobic and anaerobic resources, and shows that the metabolic costs associated with the recovery from the anaerobic perturbation (i.e., EPOC) may constitute the majority of the swimming costs. The results highlight the importance of measuring both exercise MO_2 and EPOC to estimate the total metabolic costs of swimming in fish approaching prolonged and burst



swimming speeds. In the absence of EPOC measurements, the metabolic cost of swimming may be significantly underestimated.

This study shows that the onset of burst-assisted swimming is closely related to the onset of EPOC at increasing swimming speeds in individual fish. The initiation of burst swimming is therefore a strong predictor of EPOC and anaerobic metabolism. Similarly, we found that the magnitude of EPOC increases linearly with the number of bursts. The present data are consistent with a previous study on *E. lateralalis* (Svendsen et al., 2010). Combining the two data sets suggests that each burst corresponds to an energetic cost of $0.53 \text{ mg O}_2 \text{ kg}^{-1}$. *E. lateralalis* is a labriform swimmer (i.e., pectoral fins used for propulsion at low and medium swimming speeds) whereas *S. aurata* is an axial swimmer (i.e., axial undulation used for propulsion). The fact that we found no differences in the two relationships between bursts and EPOC indicates that the metabolic cost of burst swimming may be similar across fish species employing disparate types of locomotion.

MS is predicted to play a major role in relation to effects of climate change, and other anthropogenic stressors including hypoxia, on aquatic exothermic animals (Claireaux and Lefrançois, 2007; Chabot and Claireaux, 2008; Guderley and Pörtner, 2010; Pörtner, 2010; Pörtner and Peck, 2010; McBryan et al., 2013; Seth et al., 2013; Di Santo, 2015). It remains uncertain,

however, to what extent intraspecific diversity in MS varies with other important physiological traits including locomotor performance. The present study measured intraspecific variation in MS and anaerobic capacity (i.e., maximal EPOC) in *S. aurata* and correlated data with individual variation in swimming performance (U_{crit}). We found no evidence that diversity in MS or anaerobic capacity correlates with U_{crit} ($P > 0.57$) indicating that other factors, including morphological (Rouleau et al., 2010) or biomechanical (Svendsen et al., 2013) traits, drive the variation in swimming performance.

It is possible that the lacking relationship between MS and U_{crit} was caused by our method of measuring MO_{2max} . Similar to previous studies (McKenzie et al., 2003; Svendsen et al., 2013; Binning et al., 2014), we used an U_{crit} protocol to measure MO_{2max} involving progressive increments in the swimming speed of 0.25 BL s^{-1} every 30 min, starting from 2 BL s^{-1} and until fatigue. Our protocol differed, however, from conventional protocols, because we inserted periods with swimming speeds adjusted to 0.5 BL s^{-1} (acclimation speed) for measurements of EPOC after each swimming speed $\geq 2 \text{ BL s}^{-1}$. Although the mechanistic basis is unknown, it is possible that our protocol affected the measurements of MO_{2max} . As an alternative to the U_{crit} protocol, a number of recent studies have used a chase protocol to measure MO_{2max} (Norin and Malte, 2011, 2012; Svendsen et al., 2014). The U_{crit} protocol is often assumed to provide measures of MO_{2max} (Farrell and Steffensen, 1987; Hammer, 1995) and may in fact elicit values of MO_{2max} that are higher than the values elicited by the chase protocol (Roche et al., 2013). Therefore, it is unlikely that a significant relationship between MS and swimming performance would have been revealed if we had used a chase protocol instead of the U_{crit} protocol to measure MO_{2max} . In humans, MO_{2max} is typically measured using test protocols that are much faster (Barker et al., 2011; Vanhatalo et al., 2011; Mauger et al., 2013) than the U_{crit} protocol used in the present study. While a protocol that continuously steps up the swimming speed in much faster pace than the U_{crit} protocol might produce higher values of MO_{2max} (and therefore MS) and swimming performance (Farrell, 2008), it remains to be tested if the methodology would produce a significant relationship between MS and swimming performance. A faster protocol would rely more on anaerobic metabolism to power swimming (Farrell, 2008; Poulsen et al., 2012), and so a relationship between anaerobic capacity and swimming performance might be revealed.

A recent study emphasized a trade-off between U_{sus} and COT_{min} driving morphological diversity in aquatic locomotion (Tokić and Yue, 2012). The trade-off assumes constraints in optimizing U_{sus} and COT_{min} simultaneously, suggesting that aquatic species may optimize either U_{sus} or COT_{min} . By applying the trade-off, Tokić and Yue (2012) modeled morphological variation and reported congruent morphological variation in several extant aquatic species. The present study examined the trade-off within two teleost species and found no support for the trade-off. In fact, data revealed a significant negative correlation between U_{sus} and COT_{min} , suggesting that individuals with high U_{sus} also exhibit low COT_{min} . The negative relationship indicates that the two traits are optimized simultaneously and could be related to the same mechanistic basis without constraints. Interestingly, studies

are increasingly uncovering significant intraspecific variation in locomotor performance and metabolic rate (Nelson et al., 2003; Langerhans, 2008, 2009a; Dalziel et al., 2011, 2012; Dalziel and Schulte, 2012; Svendsen et al., 2013; Binning et al., 2014). The present study indicates that intraspecific morphological variation, associated with intraspecific variation in locomotor performance and metabolic rate, is not driven by a trade-off between U_{sus} and COT_{min} .

There are a number of reasons why we may not observe a trade-off between U_{sus} and COT_{min} in our intraspecific data. Variation between species is much more pronounced than between individuals of the same species. Therefore, interspecific variation may better reflect the full spectrum of functional trade-offs that influences morphological variation related to aquatic locomotion. It is also possible that a trade-off between U_{sus} and COT_{min} is present in the two tested fish species, but not expressed at the whole-organism level, because of compensating or masking factors involving morphological, physiological and/or biomechanical traits. Moreover, our estimates of U_{sus} and COT_{min} based on respirometry and video analysis might be misleading. For example, it is possible that estimates of U_{sus} using measures of EPOC (*S. aurata*) and burst-assisted swimming (*P. reticulata*) do not accurately reflect maximum sustained swimming speeds. MO_2 is, however, a well-established proxy for aerobic metabolic rate, and the gait transition from steady to unsteady (i.e., burst-assisted) swimming is a well-known indicator of the shift from aerobic to anaerobic power production (Peake and Farrell, 2004, 2006; Peake, 2008; Svendsen et al., 2010). Similarly, it is possible that the use of forced linear swimming to estimate U_{sus} and COT_{min} provides results that do not necessarily reflect natural conditions, because fish typically swim spontaneously in a non-linear fashion with the relationship between swimming speed and metabolic rate differing from linear swimming (Steinhausen et al., 2010).

Diversity in locomotor performance and metabolism can be important sources of variation in animal behaviors. For example, Hillman et al. (2014) suggested that variation in physiological capacity for movement influences dispersal and therefore fine-scale genetic structure of several vertebrate groups. At the intraspecific level, physiological performance is an important determinant of behaviors related to schooling (Killen et al., 2011), territory acquisition and defense and foraging (Breau et al., 2011; Killen et al., 2014). Likewise, physiological and energetic states may influence behaviors in migratory species (Poulsen et al., 2010; Boel et al., 2014). Recent studies have shown that exercise training that increases swimming performance may change the behavior of animals and cause elevated boldness and exploratory tendency (Sinclair et al., 2014). The mechanistic basis of the relationship between exercise training and behavior could be related to the positive relationship between U_{sus} and U_{opt} found in the present study. Because exercise training increases aerobic potentials in red and white musculature (Davison, 1997) and swimming performance (Farrell et al., 1990; Sinclair et al., 2014), exercise training should also elevate U_{sus} and therefore U_{opt} . Typically, fish swim spontaneously at speeds corresponding to U_{opt} (Videler, 1993; Tudorache et al., 2011). This hypothesis suggests that exercise training increases spontaneous swimming speeds via the

positive relationship between U_{sus} and U_{opt} . It seems likely that increased spontaneous swimming speed is associated with elevated boldness and exploratory tendency as observed by Sinclair et al. (2014). Therefore, the positive relationship between U_{sus} and U_{opt} could provide a mechanistic link between physiological and behavioral phenotypes. Nevertheless, this hypothetical framework warrants additional study to clarify the mechanistic basis of intraspecific correlations between physiological and behavioral phenotypes.

AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: BT, JCS, JFS. Performed the experiments: BT. Analyzed the data: JCS, GAC, BT. Contributed reagents/materials/analysis tools: JFS. Wrote the paper: JCS. Revised the manuscript critically for important intellectual content: JCS, BT, GAC, JFS.

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